Coral Reefs (2018) 37:527–532
https://doi.org/10.1007/s00338-018-1677-y

NOTE

Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals

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Received: 21 September 2017 / Accepted: 14 March 2018 / Published online: 19 March 2018

Abstract Coral bleaching events have caused extensive mortality on reefs around the world. Juvenile corals are generally less affected by bleaching than their conspecific adults and therefore have the potential to buffer population declines and seed recovery. Here, we use juvenile and adult abundance data at 20 sites encircling Lizard Island, Great Barrier Reef, before and after the 2016 bleaching event to quantify: (1) correlates of changes in juvenile abundance following a bleaching event; (2) differences in susceptibility to extreme thermal stress between juveniles and adults. Declines in juvenile abundance were lower at sites closer to the 20-m-depth contour and higher for *Acropora* and *Pocillopora* juveniles than for other taxa. Juveniles of *Acropora* and *Goniastrea* were less susceptible to bleaching than adults, but the opposite was true for *Pocillopora* spp. and taxa in the family Merulinidae. Our results indicate that the potential of the juvenile life stage to act as a buffer during bleaching events is taxon-dependent.

Keywords Coral reefs · Climate change · Ecology · Thermal stress · Juvenile corals

Introduction

Coral reefs have been facing numerous anthropogenic stressors for decades, leading to a severe decline in the abundance of corals and associated organisms on reefs (Jackson et al. 2001). Among those stressors, increasing atmospheric carbon dioxide concentrations have had a strong negative effect on coral health by causing rapid and prolonged increases in sea surface temperatures that, in combination with high solar radiation, disrupt the relationship between the coral host and photosynthetic endosymbiotic algae (Lesser et al. 1990). Thermal bleaching often results in partial colony mortality or death (Harriott 1985), but the severity of bleaching depends on many factors. Importantly, juvenile corals tend to bleach less and survive better than adults (Mumby 1999; Shenkar et al. 2005; Loya et al. 2001) and therefore have the potential to facilitate post-bleaching recovery.

A few explanations for the difference in bleaching susceptibility between juveniles and adults have been proposed. First, mass transfer to eliminate toxic by-products occurs more rapidly in small organisms than in large ones (Nakamura and van Woesik 2001) and in flat rather than branching organisms (Patterson 1992). Juvenile corals are both small and relatively flat, and mass transfer dynamics

Topic Editor Dr. Anastazia Banaszak

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00338-018-1677-y) contains supplementary material, which is available to authorized users.

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might at least partly explain their lower susceptibility to bleaching. Additionally, differences between juvenile and adult susceptibilities to bleaching might be partially driven by higher concentrations of fluorescent proteins in juveniles (Papina et al. 2002), which enhance resistance to coral bleaching by dissipating excess light energy (Salih et al. 2000). Moreover, being non-reproductive might allow juveniles to invest more energy into maintenance to survive thermal stress when compared to adults.

Responses to thermal stress can differ widely between corals and environments. Some coral taxa are more susceptible to bleaching than others (Marshall and Baird 2000; Loya et al. 2001). Structural complexity can also be important because it increases variation in irradiance (Brakel 1979). High irradiance worsens the effects of high water temperatures on coral health (Lesser et al. 1990) and therefore colonies in shaded microhabitats typically bleach less (Hoogenboom et al. 2017; Muir et al. 2017). High water flow facilitates the removal of toxins produced at high water temperatures and high irradiance, reducing bleaching-induced mortality (Nakamura and van Woesik 2001) and facilitating post-bleaching recovery (Nakamura et al. 2003). This experimental work is supported by field work indicating that sites close to deeper water were more resistant to bleaching on the Great Barrier Reef (GBR) in 2002, presumably due to proximity to cooler water and a greater capacity for water mixing (Done et al. 2003).

Warm water temperatures in the austral summer of 2016 led to the most severe bleaching event on record on the GBR and caused widespread mortality, particularly in the northern section of the GBR (Hughes et al. 2017). We use environmental data and juvenile and adult abundance before and after the 2016 bleaching event to answer the following questions: (1) What are the best environmental predictors of changes in juvenile abundance after a bleaching event? (2) Per taxon, are adult or juvenile colonies more resistant to extreme thermal disturbance?

Methods

Study location and data collection

Data were collected at 20 sites around Lizard Island in the northern GBR (14.6688°S, 145.4594°E) in November in each of 2015 and 2016 (Fig. 1). At each site, five quadrats of 1 or 0.81 m^2 (in 2015 and 2016, respectively) were haphazardly placed and all juvenile corals within them were counted and identified to genus following Veron (2000) but updating genus and family following the World Register of Marine Species. Colonies with a maximum diameter < 5 cm were considered to be juveniles (sensu Bak and Engel 1979). Fragments were not considered juveniles. Five or six 10-m line-intercept transects were laid at each site to record abundances of adult corals (≥ 5 cm diameter). Abundance was the number of individual colonies that were intercepted by the transect tape.

Predictor variables

We tested the extent to which bleaching susceptibility measured by changes in abundance was predicted by five factors: thermal stress, rugosity, aspect, distance to the 20-m-depth contour, and taxon (Table A1). We used site-level maximum water temperature recorded by temperature loggers at the sites from November 2015 to 2016 as a proxy for thermal stress (Done et al. 2003). Rugosity was used as a proxy for structural complexity and was estimated from 3-D reconstructions of 130 m^2 areas within each site in 2015 (Pizarro et al. 2017). Rugosity was defined as the ratio of the site's 3-D surface area to the 2-D area of the plane of best fit (Friedman et al. 2012). Sites differ in water currents and wind exposure depending on their location around the island; therefore, aspect (NW, NE, SW, SE) was included as a variable to capture these differences. Sites close to the 20-m-depth contour (m, log scale) are expected to have a greater proximity to deep and presumably cooler water and a greater capacity for water mixing than sites farther away (Done et al. 2003). Finally, taxonomic category was also included as a variable (Marshall and Baird 2000).

Analysis

To test whether juvenile abundance per m^2 decreased in 2016 relative to 2015, we fitted a linear mixed effects model with year as a fixed effect and site as a random effect ('lme4' R package; Bates et al. 2015). To examine the best predictors of change in juvenile abundance (number of juveniles), we calculated the yearly mean abundance (m^{-2}) for each taxonomic category at each site. Genera with fewer than 20 juveniles were grouped with other genera with fewer than 20 individuals belonging to the same family. Family groups with fewer than 20 juveniles were eliminated to ensure estimates for juvenile change were not strongly influenced by rare taxa. We fitted a series of linear models predicting proportional change in juvenile abundance between years for taxonomic category i at site j ($\log_{10}$ (abundance 2016_{ij}/abundance 2015_{ij})) as a function of each combination of predictor variables. Our sample size allowed for a maximum of two predictor variables to be included in each model. We included models with site as a random effect and without random effects, and we calculated the R^2 value for each model ('r2glmm'; Jaeger et al. 2016).

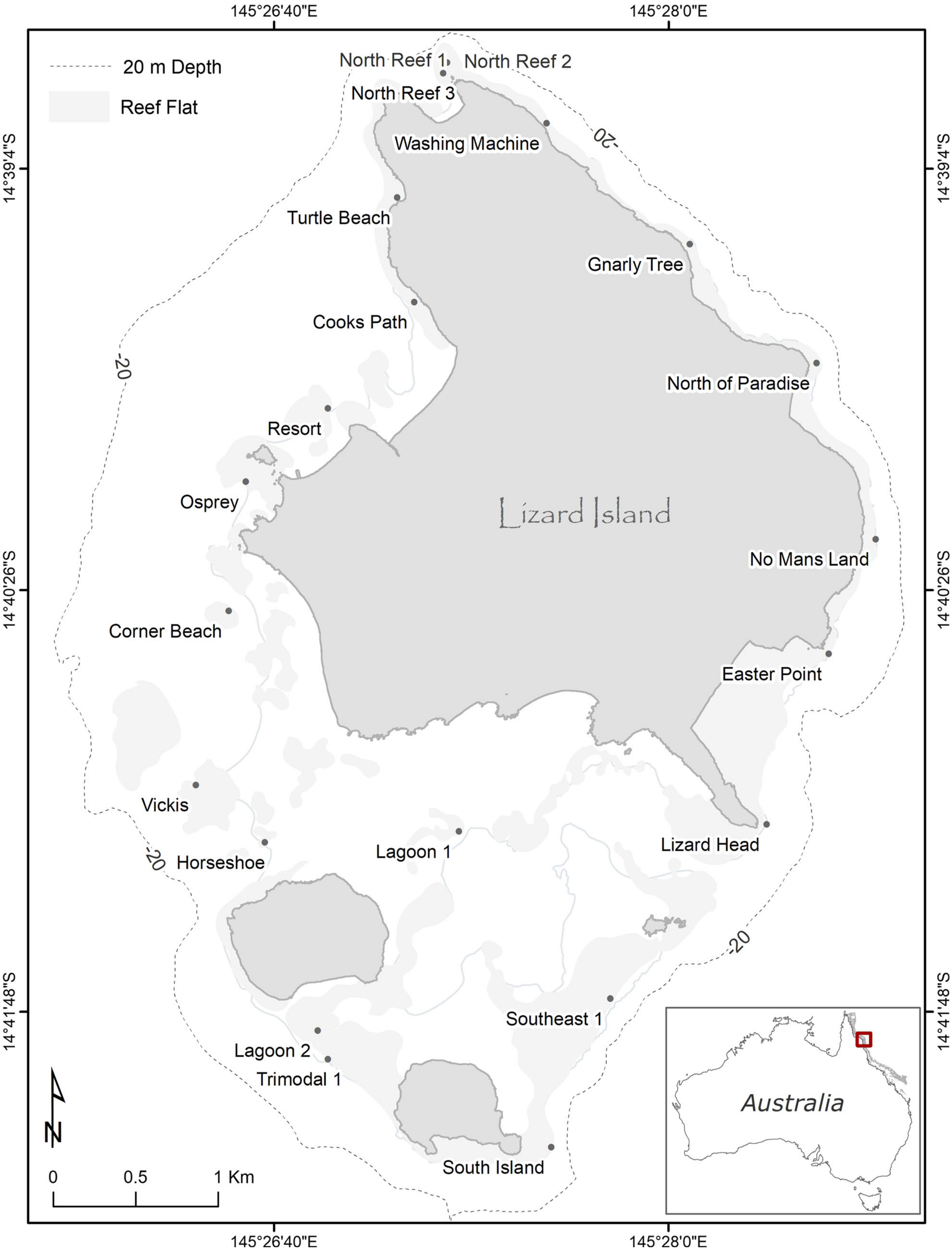

Fig. 1 Map of Lizard Island showing the sites that were surveyed. Dotted lines show the 20-m-depth contour

To examine the similarity of changes in abundance post-bleaching between juveniles and adults, we plotted mean proportional change in adults versus mean proportional change in juveniles for each taxon, using changes in proportional abundance as a proxy for mortality. All analyses were performed in R version 3.2 (R Core Team 2016).

Results and discussion

Total mean juvenile abundance from did not vary significantly between 2015 and 2016 at the island scale (Table A2) and changes among sites were highly variable (Fig. A1). Proportional change in juvenile abundance was best explained by distance to the 20-m-depth contour and taxonomic category (Table A3; site as a random effect was not significant: *p* value = 1).

Proportional change in juvenile abundance decreased in 2016 relative to 2015 with increasing distance to the 20-m-depth contour (Fig. 2a; Table A4). Sites closer to the 20-m-depth contour are closer to deeper and potentially cooler water, as well as having a higher capacity for these waters to mix due to the greater angle of the reef slope (Done et al. 2003). On Lizard Island, sites closer to the 20-m-depth contour are on the eastern side of the island and therefore are also more exposed to the south-easterly trade winds that will stimulate water mixing and movement (Fig. A2). Moreover, high water flow facilitates the mass transfer of toxic by-products of bleaching (Nakamura and van Woesik 2001), ameliorating the effects of bleaching. In contrast, Hoogenboom et al. (2017) attributed their finding that bleaching severity was higher in adults at sites that were closer to open water on Lizard Island to the fact that these sites experience less temperature variability, a factor known to promote thermal tolerance in adults (Oliver and Palumbi 2011). These contrasting results between adult and juveniles suggest that factors associated with bleaching susceptibility differ among life stages.

Some previous studies have suggested that juveniles are ‘immune’ to the effects of bleaching (e.g. Mumby 1999; Depczynski et al. 2013). In contrast, our results reveal an order of magnitude decline in the abundance of *Pocillopora* and *Acropora* (Fig. 2b) and lesser, but still significant, declines in *Dipsastraea, Favites* and other Merulinidae (Fig. 2b). Mumby (1999) conducted his research in Belize, were there are no *Pocillopora,* and *Acropora* colonies are rare: juveniles of these genera were the most susceptible to bleaching at Lizard Island. Therefore, the contrasting results are most likely driven by differences in species composition. Depczynski et al. (2013) used a different size cut-off for juveniles (less than 10 cm vs. our 5 cm). In addition, their estimates of mortality were based on the proportion of individuals in different categories a few months post-bleaching (i.e. dead vs. alive). In fact, it is often difficult to detect dead coral colonies, particularly when they are small; therefore, it is possible they underestimated mortality in the juvenile size class.

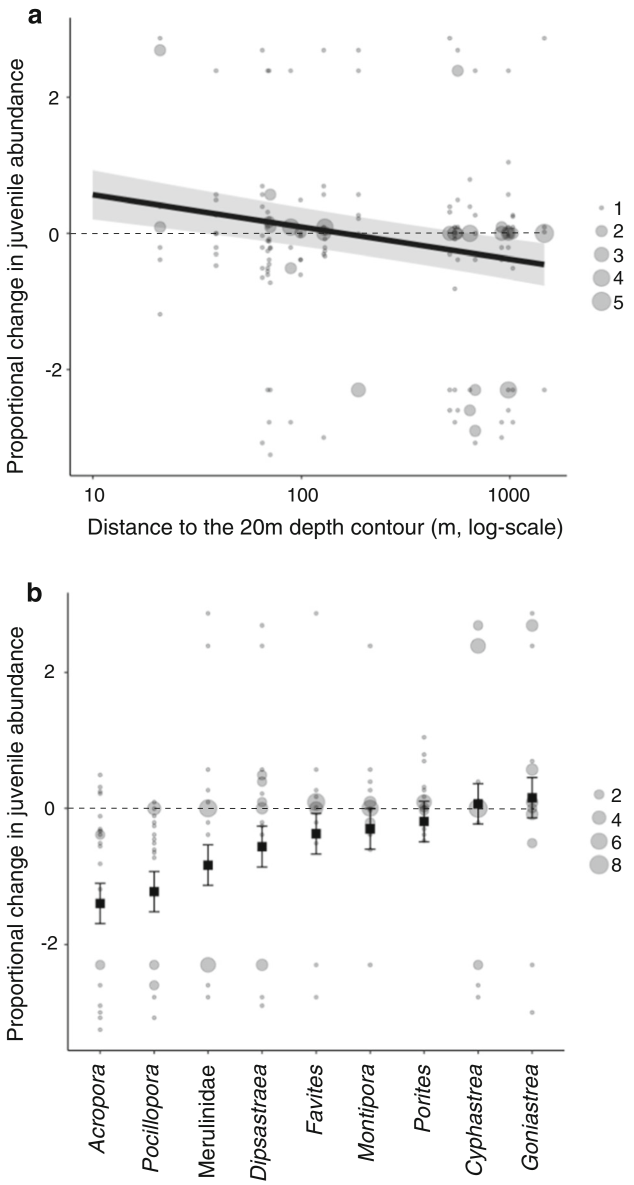

Fig. 2 Panel a—proportional change in juvenile abundance ($\log_{10}$ [$\text{abundance}_{2016}/\text{abundance}_{2015}$]) as a function of distance to the 20-m-depth contour (m). The black line shows the predicted proportional change in juvenile abundance, and the grey ribbon shows 95% confidence intervals. Panel b—proportional change in juvenile abundance ($\log_{10}$ [$\text{abundance}_{2016}/\text{abundance}_{2015}$]) for each taxonomic category. Error bars show standard errors. Grey dots represent observed data, with the dot size showing the number of observations

Overall, the percentage of variation in the proportional change of juvenile abundance explained by any combination of two or fewer variables was low (Table A3). More than one cohort of corals correspond to the juvenile size class in this study. Juvenile abundance is ultimately increased by recruitment and decreased by juveniles dying or growing larger than 5 cm. While bleaching can affect juvenile survival, many other factors, such as the strength of yearly recruitment and the bleaching-independent mortality, will also contribute to changes in juvenile abundance.

Differences in susceptibility to the 2016 bleaching event between juveniles and adults differed among taxa (Fig. 3). Total mean abundance of *Cyphastrea, Porites*, *Montipora*, *Favites*, and *Dipsastraea* spp. remained stable in both life stages. Overall, adults of *Acropora* and *Goniastrea* spp. were more affected than juveniles (mean abundance of *Goniastrea* juveniles actually increased; Fig. A3), a finding consistent with previous studies (Mumby 1999; Loya et al. 2001; Bena and van Woesik 2004; Depczynski et al. 2013). However, juveniles of *Pocillopora* spp. and the family Merulinidae had a stronger decline in abundance post-bleaching than adults, indicating that the decrease in susceptibility as a function of size is taxon-dependent.

Demographic processes of juvenile corals have important effects on population dynamics and are key to population persistence after disturbance (Connell et al. 1997). Our results show that differences in bleaching susceptibility between juveniles and adults among taxa need to be considered when predicting changes to reef communities following episodes of thermal stress.

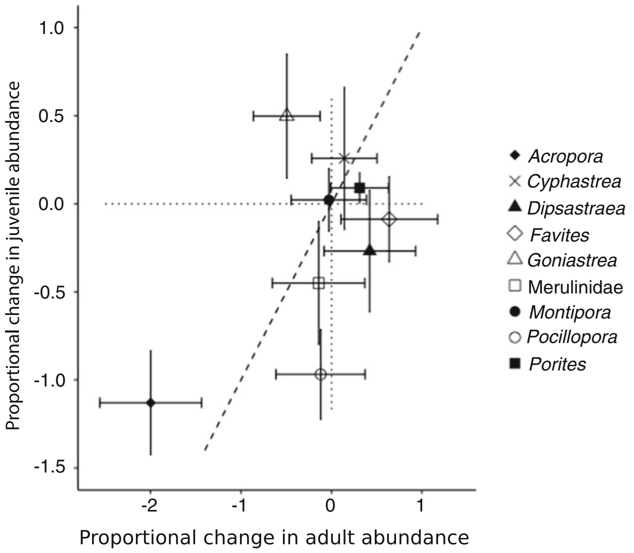

Fig. 3 Proportional change in adult abundance versus proportional change in juvenile abundance (log–log scale) between 2015 and 2016 for each taxonomic category. Line ranges indicate standard errors. The dotted vertical and horizontal lines indicate no proportional change in adult and juvenile abundance, respectively, between years. The dashed line indicates values for which the proportional change in adult abundance is equal to the proportional change in juvenile abundance

Acknowledgements We thank the Lizard Island Research Station staff for their support. We thank two anonymous reviewers for their constructive feedback. Funding was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies (CE140100020) and the Templeton Foundation (Grant #60501, 'Putting the Extended Evolutionary Synthesis to the Test'). MD is grateful to the Scottish Funding Council (MASTS, grant reference HR09011) and the European Research Council (grant BioTIME). The study was partially supported by Australian Research Council grants DP1093448 and FT110100609.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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